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RECEPTIVE FIELDS AND FUNCTIONAL ARCHITECTURE OF MONKEY STRIATE CORTEX

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SUMMARY

1. The striate cortex was studied in lightly anaesthetized macaque and spider monkeys by recording extracellularly from single units and stimulating the retinas with spots or patterns of light. Most cells can be categorized as simple, complex, or hypercomplex, with response properties very similar to those previously described in the cat. On the average, however, receptive fields are smaller, and there is a greater sensitivity to changes in stimulus orientation. A small proportion of the cells are colour coded.

2. Evidence is presented for at least two independent systems of columns extending vertically from surface to white matter. Columns of the first type contain cells with common receptive-field orientations. They are similar to the orientation columns described in the cat, but are probably smaller in cross-sectional area. In the second system cells are aggregated into columns according to eye preference. The ocular dominance columns are larger than the orientation columns, and the two sets of boundaries seem to be independent.

3. There is a tendency for cells to be grouped according to symmetry of responses to movement; in some regions the cells respond equally well to the two opposite directions of movement of a line, but other regions contain a mixture of cells favouring one direction and cells favouring the other.

4. A horizontal organization corresponding to the cortical layering can also be discerned. The upper layers (II and the upper two-thirds of III) contain complex and hypercomplex cells, but simple cells are virtually absent. The cells are mostly binocularly driven. Simple cells are found deep in layer III, and in IV A and IV B. In layer IV B they form a large proportion of the population, whereas complex cells are rare. In layers IV A and IV B one finds units lacking orientation specificity; it is not clear whether these are cell bodies or axons of geniculate cells. In layer IV most cells are driven by one eye only; this layer consists of a mosaic with

cells of some regions responding to one eye only, those of other regions responding to the other eye. Layers V and VI contain mostly complex and hypercomplex cells, binocularly driven.

5. The cortex is seen as a system organized vertically and horizontally in entirely different ways. In the vertical system (in which cells lying along a vertical line in the cortex have common features) stimulus dimensions such as retinal position, line orientation, ocular dominance, and perhaps directionality of movement, are mapped in sets of superimposed but independent mosaics. The horizontal system segregates cells in layers by hierarchical orders, the lowest orders (simple cells monocularly driven) located in and near layer IV, the higher orders in the upper and lower layers.

INTRODUCTION

Over the past ten years we have studied the sequential processing of visual information in the cat by examining the responses of single cells at various points along the visual pathway. In extending this work it seemed natural to turn to the monkey, an animal that comes close to man in its visual capabilities, especially its high acuity and well developed colour vision. In contrast with the cat, moreover, most primates have a visual pathway that is further differentiated, with a rod-free fovea, a six-layered geniculate, and a striate cortex that lends itself well to studies of functional architecture, being conspicuously laminated and well demarcated from neighbouring cortical areas.

In this paper we present the results of a series of recordings from the monkey striate cortex. The study may be regarded as a continuation of previous work on the monkey optic nerve (Hubel & Wiesel, 1960) and lateral geniculate body (Wiesel & Hubel, 1966). The early experiments were done in the cortex of the spider monkey (*Ateles*), but the rhesus (*Macaca mulatta*) was used in all of the more recent work.

METHODS

Six spider monkeys and sixteen macaques were used. Details of stimulating and recording procedures have been published elsewhere (Hubel & Wiesel, 1962; Wiesel & Hubel, 1966). Animals, 2–3 kg in weight, were anaesthetized with thiopental sodium, and light anaesthesia was maintained throughout the experiment. Since intravenous succinylcholine alone was often insufficient to prevent all eye movements, gallamine triethiodide (2–3 mg/kg) was also usually given intramuscularly at half-hour intervals.

When only one or two penetrations were planned in a single animal, a small hole was drilled in the skull, the dura incised keeping the arachnoid intact, and the electrode introduced through a hollow 19-gauge stainless-steel needle, which was cemented into the hole to make a closed chamber. In a few experiments designed to explore a wider area of cortex a modified Davies chamber was cemented to the skull (Hubel & Wiesel, 1963). Microelectrodes were sharpened tungsten wire insulated with a clear vinyl lacquer (Hubel, 1957).

To help reconstruct the electrode tracks, one or several lesions were made in each penetration by passing direct current through the electrode (Hubel, 1959). In the monkey cortex 2 μA for 2 sec (electrode negative) was usually sufficient. All brains were fixed in formalin, photographed, embedded in celloidin, sectioned serially at 20 μ, and stained for Nissl substance with cresyl violet.

RESULTS

PART I. *Receptive Field Types*

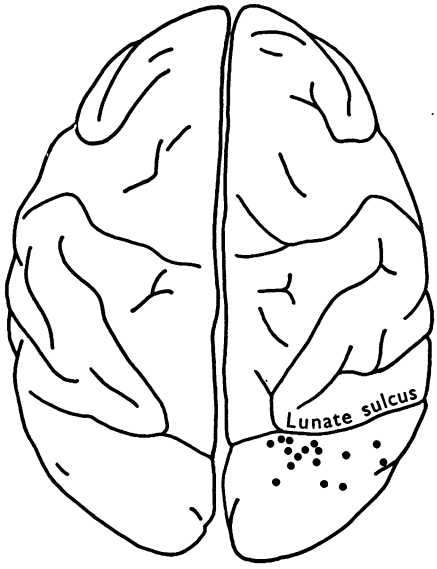
This study is based upon recordings of 150 cells in seven penetrations in six spider monkeys, and 272 cells in twenty-five penetrations in sixteen macaque monkeys. Most of the penetrations were made in cortical regions subserving the 0–4° parafoveal region; a few passed through buried cortical folds subserving the mid or far periphery, and in two laterally placed penetrations the fields were in the fovea. The approximate recording sites in the sixteen rhesus experiments are shown for a representative brain in Text-fig. 1.

We begin by describing the various types of receptive fields that can be distinguished in the monkey striate cortex, emphasizing especially any differences between monkey and cat. Implicit in these descriptions is the possibly over-simplified concept of a hierarchical system dependent on anatomical wiring, in which geniculate cells with concentric fields converge on simple cortical cells, simple cells in turn converge upon complex cells, and complex on hypercomplex. The evidence for such connexions (Hubel & Wiesel, 1962, 1965*a*) is derived from the properties of the fields themselves, and also from the functional architecture of the cortex.

Simple cells. As in the cat, these cells are defined as having receptive fields with spatially distinct 'on' and 'off' areas separated by parallel straight lines (Hubel & Wiesel, 1959). Twenty-five of the 272 cells studied in rhesus were definitely established as simple, and a similar proportion was seen in the spider monkey. This small number almost certainly does not reflect the actual proportion of simple cells in striate cortex, since judging from spike size and difficulties in isolation these cells are mostly small. Moreover, some penetrations stopped short of the layers where simple cells are most populous. In a typical penetration through the full cortical thickness, when the electrode was fine enough to isolate cells easily, three or four out of thirty or so cells could be expected to be simple. An example of such a penetration is described in detail in the next section.

Even in this small sampling, we found representatives of all of the 'simple' receptive field subtypes described in the cat (Hubel & Wiesel, 1962, Fig. 2). The commonest simple fields were those with long narrow 'on'-centres sandwiched between two more extensive 'off' regions, and those with an 'on' and an 'off' region lying side by side, but a few examples of each of the other types were also seen. Knowing the exact configuration

of a field made it possible to predict the optimum stimulus: its size, shape, orientation, and position on the retina. As described below, and in contrast with what we found in the cat, most simple cells were driven by one eye only. Six of the twenty-five cells showed opponent-colour properties, suggesting that the proportion of colour coded cells may be higher in simple cells than in complex.

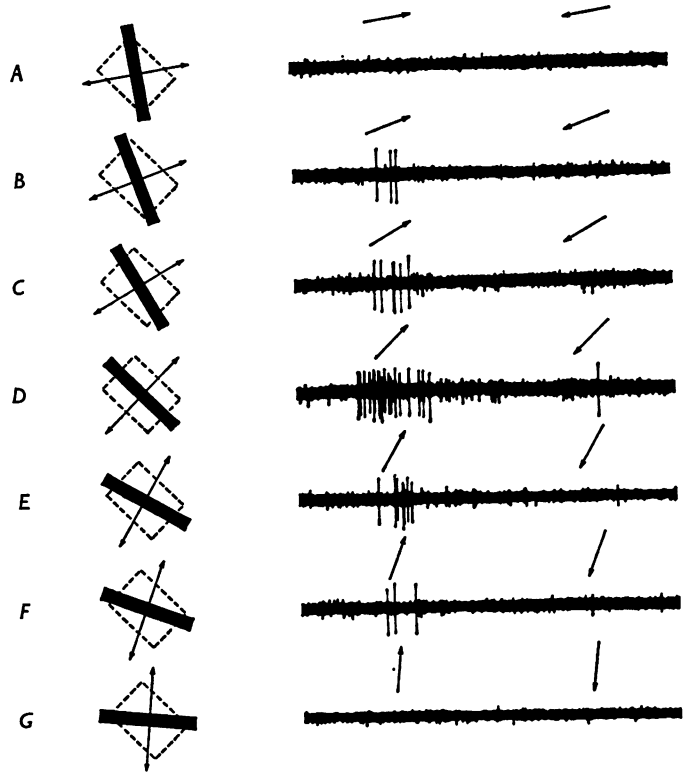


Text-fig. 1. Recording sites for the sixteen rhesus experiments. Diagram of monkey brain viewed from above; anterior is up. Many of the dots represent several closely spaced penetrations in a single monkey. Several deep penetrations went into buried folds of striate and non-striate cortex.

Complex cells. Complex cells are the commonest of all types, making up 177 of the 272 cells in the rhesus. The properties of these cells were similar to those we have described for the cat (Hubel & Wiesel, 1962). By definition, there was no separation of receptive fields into excitatory and inhibitory parts. As for simple cells, a line stimulus (slit, dark bar, or edge) in a particular orientation evoked optimum responses, and as the orientation was varied the responses fell off, usually failing long before an angle 90° to the optimum was reached. Prolonging the line in either direction did not reduce the response. But whereas for the simple cell the position of the stimulus was crucial, in the complex a response was evoked on shining the correctly oriented line on any part of the field, or by moving the line over the field. As in the cat, about half of the cells showed highly asymmetrical responses to diametrically opposite directions of movement, while the rest

showed little or no directional preference. Even when responses were highly asymmetrical, the less effective direction of movement usually evoked some minimal response (see Text-fig. 2), but there were a few examples in which the maintained activity was actually suppressed.

Individual complex cells differed markedly in their relative responsiveness to slits, edges, or dark bars. The majority responded very much better to one than to the other two, but some reacted briskly to two of them, and a few to all three. For a cell that was sensitive to slits, but not to edges, the



Text-fig. 2. Responses of a complex cell in right striate cortex (layer IV A) to various orientations of a moving black bar. Receptive field in the left eye indicated by the interrupted rectangles; it was approximately $\frac{3}{8} \times \frac{3}{8}°$ in size, and was situated 4° below and to the left of the point of fixation. Ocular-dominance group 4. Duration of each record, 2 sec. Background intensity 1·3 $\log_{10}$ cd/m², dark bars 0·0 log cd/m².

responses increased as slit width was increased up to some optimal value, and then they fell off sharply; the optimum width was always a small fraction of the width of the whole field. For complex cells that responded best to edges, some reacted to one configuration and also to its mirror

image, while others responded only to one edge configuration. In the first type a broad slit or dark bar usually gave more vigorous responses than an edge, as though it combined the advantages of the two types of edge. On narrowing the stimulus down to a width that might be close to the optimum for the usual slit or dark-bar complex cell, the response usually failed. Presumably the two types of cells are connected to simple cells in entirely different ways.

A complex cell that responded best to a moving dark bar is illustrated in Text-fig. 2. Here the optimally oriented stimulus (Text-fig. 2*D*) gave very different responses to the two different directions of movement, with a minimal, inconstant discharge to movement down and to the left. The rate of decline of this cell's responses as the stimulus orientation deviated from the optimum was fairly typical; while the decline varied to some extent from cell to cell (see below), it was generally steeper in the monkey than in the cat. Most field orientations could be specified to within 5–10°, as compared to 10–15° in the cat.

Hypercomplex cells. Fifty-three of the 272 cells recorded from the rhesus were lower-order hypercomplex. For these, extending the line (slit, edge or dark bar) beyond the activating part of the receptive field in one or both directions caused a marked fall-off in the response, and there was usually no response at all if the line was made long enough. The proportion of hypercomplex cells occurring here may well be higher than our figures suggest, since in the early monkey experiments we did not know that such cells existed and did not systematically vary the lengths of the stimuli. We have recently found hypercomplex cells in the cat striate cortex, but they seem to be less common than in the monkey.

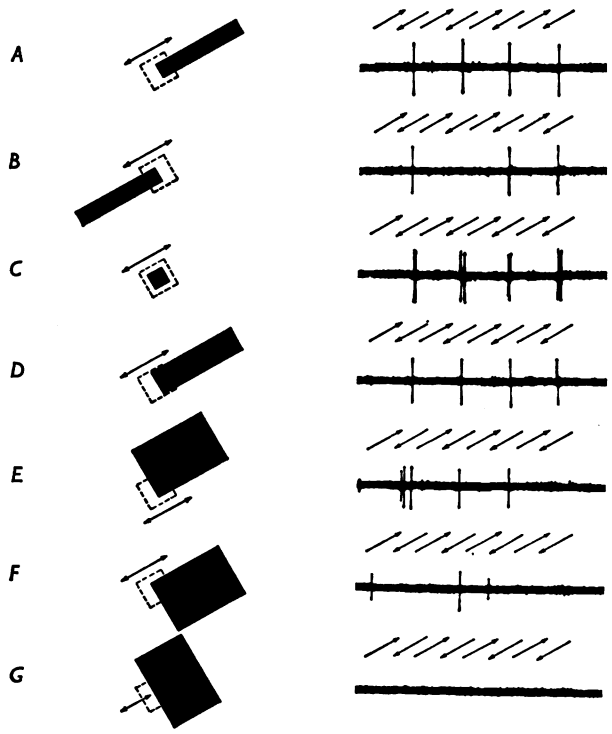
Responses of a typical hypercomplex cell are shown in Text-fig. 3. The more or less square central activating region, indicated by interrupted lines, was flanked by a weak antagonistic region above and by a stronger one below, so that to evoke a consistent response a line (edge or bar) had to be terminated within the rectangle or at its borders (Text-fig. 3*A–D*). When it extended beyond them, as in Text-fig. 3*E–G*, the response was reduced or obliterated. Another example is shown in Text-fig. 4; here the most powerful stimulus was an obliquely oriented slit moving in either direction across the region marked by broken lines. Lengthening the stimulus in both directions again greatly reduced the response, though this time the suppression was not complete.

No higher-order hypercomplex cells were seen in monkey striate cortex (Hubel & Wiesel, 1965*a*).

Sizes of receptive fields. For comparable regions of the visual field, simple receptive fields in the monkey were on the average much smaller than in the cat. At 1–4° from the centre of gaze, for example, fields ranged from

$\frac{1}{4} \times \frac{1}{4}°$ up to $\frac{1}{2} \times \frac{3}{4}°$, as against about $\frac{1}{2} \times \frac{1}{2}°$ up to about $4 \times 4°$ for the cat. Complex and hypercomplex fields in the monkey were likewise smaller than in the cat, perhaps about one quarter the size in linear dimensions. They tended to be somewhat larger than simple fields, perhaps $1\frac{1}{2}$ to 2 times as big, in linear dimensions.

In the two experiments made in the region representing the fovea one or two simple fields were less than $\frac{1}{4} \times \frac{1}{4}°$, but their exact boundaries were not determined. Surprisingly, the range of sizes of complex and hypercomplex fields was not very different from that seen a few degrees further

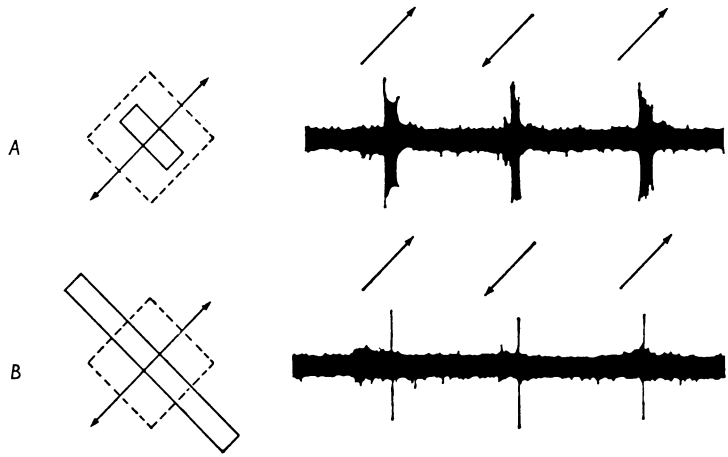


Text-fig. 3. Responses of a hypercomplex cell from layer III of monkey striate cortex. (This was cell 9 in Text-figs. 7 and 8). 'Activating' portion of receptive field ($\frac{3}{8} \times \frac{3}{8}°$) is outlined by interrupted lines. Stimulus of this region by a moving edge activates cell (*A–D*). Below this region, and to some extent above it, are regions appropriate stimulation of which suppresses the response to an edge (*E–G*). Duration of each record 5 sec. Stimulus intensities as in Text-fig. 2.

out. As we have discussed elsewhere (Hubel & Wiesel, 1962), acuity is probably not closely related to over-all receptive field dimensions, but rather to the widths of optimally shaped stimuli.

Units lacking orientation specificity. In layer IV we usually recorded monocularly driven units whose receptive fields were similar to those of

geniculate cells. The spikes of these units were small and negative, being quite different from the typical spikes of myelinated fibres seen in optic tract and radiations, and corpus callosum (Hubel, 1959; Hubel & Wiesel, 1967). The field properties and localization of these IVth layer units makes one suspect that they are axons or axon-terminals of geniculate cells, but they could be cortical cells, and it will probably be necessary to stimulate electrically the subcortical optic radiations to settle the question. Some units with concentric receptive fields had more complex responses to coloured stimuli than anything we saw in the lateral geniculate; these are discussed below.



Text-fig. 4. Hypercomplex cell recorded from right striate cortex, layer II. *A*: stimulus of left eye by moving slit within activating region ($\frac{1}{4} \times \frac{3}{8}°$); *B*: similar stimulation with slit extending beyond activating region. Background, log 0·0 cd/m²; stimulus, log 1·3 cd/m². Duration of each record 10 sec.

Cells with specific colour responses. In the rhesus lateral geniculate body the majority of the dorsal-layer cells have opponent-colour properties, light exciting them at some wave-lengths, inhibiting them at others, diffuse white light evoking little or no response (De Valois, Jacobs & Jones, 1963; Wiesel & Hubel, 1966). For cortical cells, we expected that with this input there might be a similar emphasis on wave-length discrimination. Motokawa, Taira & Okuda (1962) have in fact described opponent colour cells in monkey cortex. It was surprising to us, however, that the great majority of cells could discriminate precisely the orientation or direction of movement of a stimulus, but had no marked selectivity regarding wave-length. There were interesting and striking exceptions to this, which are described below, but on the whole the colour responses seen in area 17 have been disappointing: for a high proportion of cells the response to a

given stimulus shape was qualitatively the same—firing being increased or firing being suppressed—regardless of wave-length, and the optimum stimulus shape was independent of wave-length. Even in the two penetrations in the region representing fovea most cells seemed to be relatively unconcerned with colour, though here the proportion of cells with colour specific responses seemed higher than it was 2–4° from the fovea.

Of the twenty-five simple cells recorded in rhesus, six had more specific colour-coded behaviour, the excitatory and inhibitory parts of the receptive field differing in spectral sensitivity in the manner of geniculate Type I cells (Wiesel & Hubel, 1966). All six fields were similar in organization, with a long narrow excitatory region with highest sensitivity to long wave-lengths, flanked on either side by more extensive inhibitory regions with relatively greater blue-green sensitivity. These cells behaved as though they received input from a set of Type I red on-centre, green off- surround geniculate cells, the commonest variety found in the dorsal geniculate layers. Certain features of two of the cells were not so easily explained, however: one responded well to a properly positioned red slit but not at all well to a white slit; another failed to respond to diffuse white light, as expected, but also responded poorly to diffuse red. Obviously it will be necessary to sample many more cells of this type, and to study them more thoroughly.

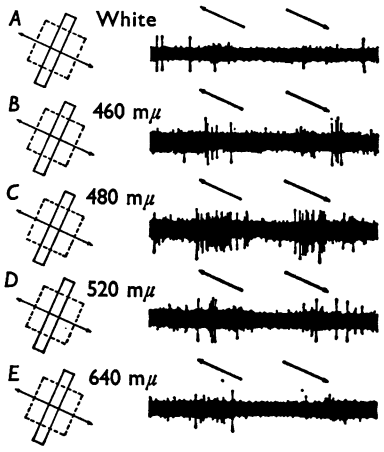
Complex and hypercomplex cells with colour selectivity. Of the 177 complex cells examined in rhesus, only twelve (about 7 %) were identified as having clear colour specificity. Not all cells were studied with monochromatic stimuli, but enough were to be reasonably sure that colour coded cells are a small minority, probably not more than 10 % for regions 2–4° from the fovea. Four cells gave responses to coloured stimuli that were qualitatively similar to their responses to white stimuli, but only over an unusually restricted band of wave-lengths. A cell might respond actively in the blue-violet (or the red), but not to light at the other end of the spectrum.

Six cells showed still more specific reactions to coloured stimuli. They responded actively to a properly oriented slit at some wave-lengths but not others, and gave little or no response to a similarly oriented white slit at any intensity. An example is illustrated in Text-figs. 5 and 6. This cell had typical complex properties, favouring up-and-left movement of a 1 o'clock oriented slit and showing no response to a slit oriented at right angles to this. The only stimuli that evoked brisk responses were blue ones, and it was striking that white slits produced by removing the interference filter from the light path were completely ineffective. The other five cells behaved in a similar way, but favoured long wave-lengths.

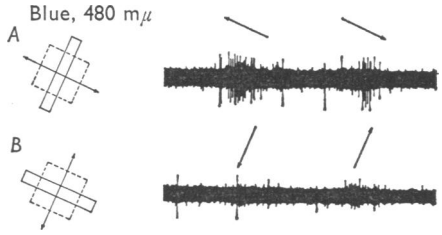
Three cells, finally, had opponent-colour properties like the ones just

mentioned, favouring monochromatic slits over white, but also had hypercomplex characteristics, in that a long slit was distinctly less effective than one of limited length.

Cells with concentric fields and dual-opponent systems. Under this heading we group a very few cells with centre-surround receptive-field organization, but with more complex behaviour than anything we have seen in



Text-fig. 5. Complex cell with colour coded properties recorded in layer II of striate cortex. Responses to movement of optimally oriented slits of white light and monochromatic light at various wave-lengths. Monochromatic light made by interposing interference filters in a beam of white light: stimulus energies are greatest for *A*, and progressively less for *E*, *D*, *C* and *B*. None of the responses was improved by lowering the intensity. Size of receptive field $\frac{1}{2} \times \frac{1}{2}°$. Ocular dominance group 1. Background and white stimulus intensities as in Text-fig. 4. Time for each record 5 sec.



Text-fig. 6. Same cell as Text-fig. 5. Responses to two orthogonal stimulus orientations at 480 mμ.

the geniculate. The fields appeared to be organized in centre-surround fashion. With centre-size spots the cells were excited by long wave-lengths and inhibited by short, with little response to white light. On the other

hand a large spot was almost completely ineffective regardless of wavelength, suggesting that the surround was red-off green-on, i.e. the reverse of the centre. It was as if two Type III (non opponent-colour) geniculate fields, an on-centre with maximum sensitivity in the red, and an off-centre with maximum sensitivity in the blue-green, had been superimposed. Since these cells were influenced from one eye only it is possible that they were axons of geniculate cells. We saw nothing this complicated in the rhesus geniculate, but our sampling there was small enough so that a relatively rare type could easily have been missed. Ganglion cells with somewhat similar fields have been described recently by Daw (1967) in the retina of the goldfish. In the units described above, however, the situation seems somewhat simpler, there being a single boundary between centre and surround instead of a separate boundary for each of the two opponent systems, as was found in the goldfish.

In summary, cells with interesting colour properties occur in the cortex but are in the minority, and, as in the geniculate, seem very diverse in type, with fields ranging in their spatial characteristics from non-oriented to hypercomplex. This survey is intended only to suggest the diversity; a satisfactory study will probably mean recording from thousands, rather than hundreds of cortical cells.

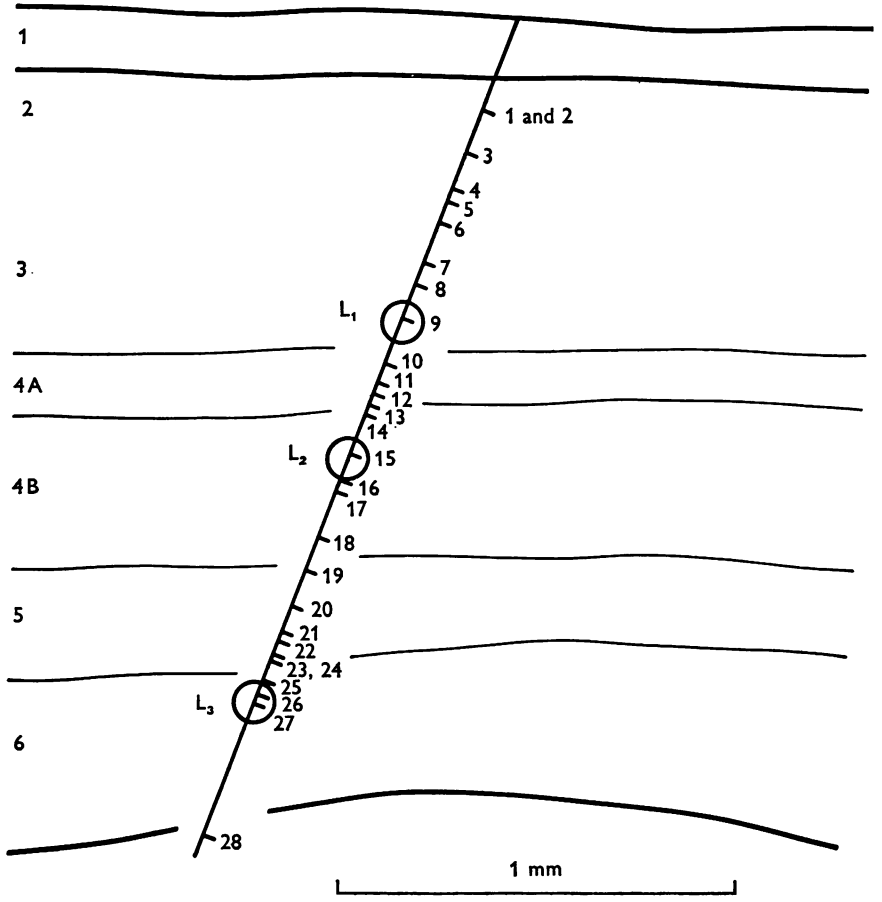
Part II. Functional Architecture

A representive penetration through striate cortex (area 17)

As shown in Fig. 1, most of the penetrations through area 17 were made from the smooth exposed part of the occipital lobe a few millimetres behind the lunate sulcus, i.e. just behind the 17–18 border, which runs parallel to and just behind the sulcus. In all rhesus experiments the brain was sectioned in the parasagittal plane, which has the advantage of intersecting the lunate sulcus and the 17–18 boundary at right angles. The convention of numbering the layers (Pl. 1) combines that of von Bonin (1942) for layers I–IV, and that of Lorente de Nó (1943) and Brodmann (1909) for V and VI. In this system each layer can be identified easily in a Nissl preparation, except for the poorly defined II–III boundary, which we place arbitrarily between the upper $\frac{1}{3}$ and the lower $\frac{2}{3}$ of the cell-rich layer making up II and III. The pale layer beneath III is termed IV A, and the alternating cell-rich, pale, and cell-rich layers are termed IV B, V, and VI.

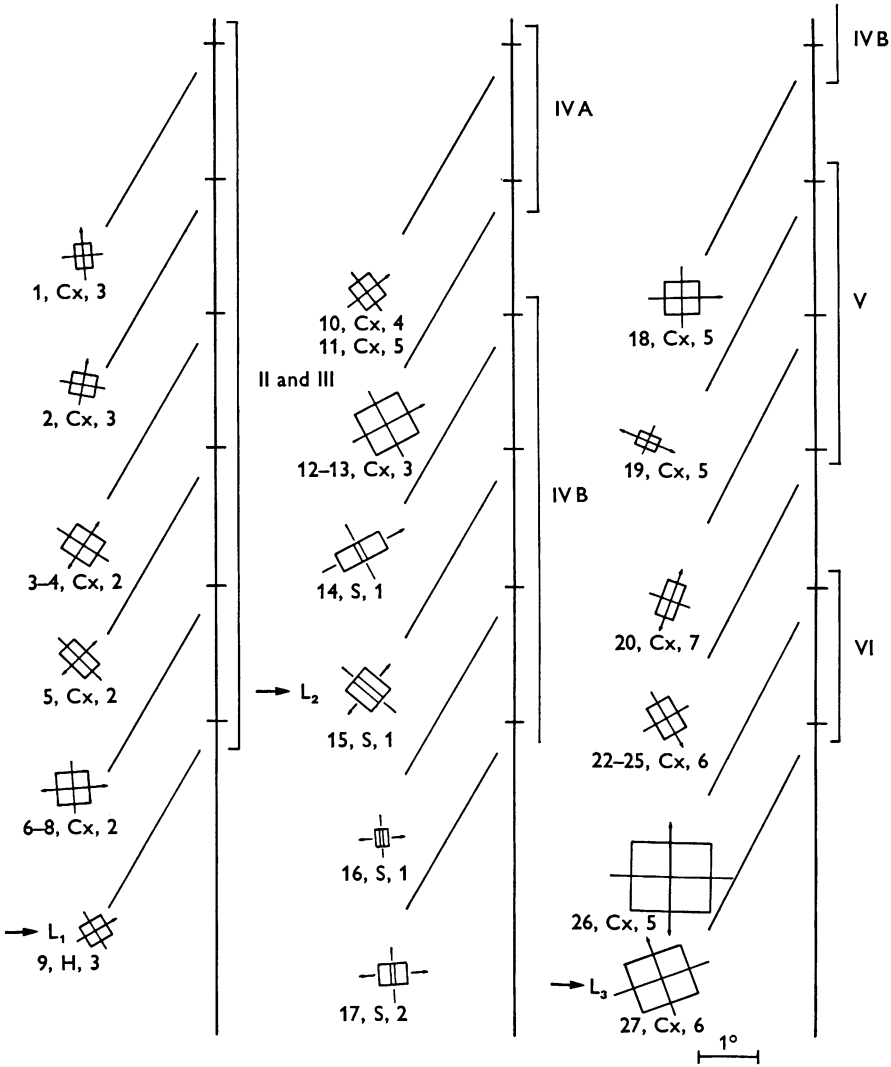
In the penetration to be described, three small lesions 50–70 μ in diameter were made at roughly $\frac{1}{2}$ mm intervals, to help estimate shrinkage during fixation and embedding, and to increase the accuracy of estimating positions of the cells encountered (Text-fig. 7; Pl. 1). Except for cells

tagged specifically by lesions, or cells very close to lesions, estimations made by this method are nevertheless only approximate. Sometimes, for example, the position of a superficial lesion corresponded poorly with depths calculated from two or more deeper lesions, possibly because of



Text-fig. 7. Positions of twenty-eight units recorded in a single penetration through rhesus striate cortex. Positions of three lesions (L_1–L_3) are indicated by circles (see also Pl. 1 and Text-fig. 8).

uneven shrinkage, or possibly due to dimpling of the cortex in the first part of some penetrations. The security with which one can assign a cell to a particular layer thus varies widely from cell to cell even in the same penetration, and statistics are difficult to compile. Specific questions can, nevertheless, often be answered with some certainty by placing lesions near cells of a particular type in penetration after penetration (see Text-



Text-fig. 8. Receptive-field diagrams for units recorded in the penetration of Text-fig. 7. Approximate positions and shapes of each field, referred to the fovea, are indicated by rectangles. Foveas are indicated separately for each field by the short horizontal lines intersecting the three long vertical lines. Responses to a moving line are shown for every field by arrows; a single arrowhead indicates strong directional preference. Square brackets refer to cortical layers. For each field the first number is the unit number; S, Cx and H mean simple, complex and hypercomplex; the last number refers to ocular-dominance groups. Cells of group 1 were driven only by the contralateral eye; for cells of group 2 there was marked dominance of the contralateral eye; for group 3, slight dominance. For cells in group 4 there was no obvious difference between the two eyes. In group 5 the ipsilateral eye dominated slightly; in group 6 markedly, and in group 7 the cells were driven only by the ipsilateral eye.

figs. 11 and 12 below). The penetration of Text-figs. 7 and 8 was exploratory, and lesions were not placed according to any particular plan.

In Text-figs. 7 and 8 the first nine cells were situated in layers II and III, lesion 1 marking the position of unit 9. Six of the nine cells were complex and, as in the cat, some showed highly asymmetrical responses to diametrically opposite directions of movement (cells 1 and 2), while the others showed no such directional preference. Cell 9 of this penetration was lower-order hypercomplex, and has already been illustrated in Text-fig. 3.

In layer IV A four complex cells were recorded, 10 and 11 responding best to dark bars, 12 and 13 to slits.

In IV B the fields of four successively recorded cells were simple in type. The second of these (unit 15) was marked by lesion 2. In three of the simple cells (14, 16, and 17) the long narrow excitatory region was most sensitive to light of long wave-lengths, with hardly any responses in the green and blue, whereas the inhibitory flanks were most sensitive in the greens and blues with little response to red. It was as if these cells had received input only from a group of red on-centre green off-surround geniculate cells. In contrast to these opponent-colour cells, unit 15, whose field was similar geometrically, seemed identical to the usual simple cell in cat cortex, with no hint of opponent colour properties.

The remaining cells in this penetration were complex. The only one with remarkable colour features was No. 20, which lacked any opponent colour properties but favoured short wave-lengths strongly, as though it had its entire input from blue-sensitive cones.

The sequence of receptive field orientations seen in this penetration was less regular than in most, but as usual there were runs of cells in which the fields all had identical orientation, for example, cells 10, 11; 12–14; 16–18. At the beginning of the penetration, the sequence of cells 1–8 is of particular interest as an example of several small shifts of field orientation all in the same direction (see below).

Many of the cells in this penetration were driven from both eyes. Cells 1–17 were dominated by the left (contralateral) eye, except for No. 11, which favoured the right eye slightly; from 18 to 27 all cells favoured the right eye. The tendency for neighbouring cells to favour the same eye was thus very pronounced, more so than is usual in the cat (Hubel & Wiesel, 1962).

This penetration illustrates several architectural features of the striate cortex which will be taken up in more detail in the remainder of the paper: (1) a tendency to aggregation of certain physiological cell types according to anatomical layering; (2) an aggregation of cells according to receptive field orientation; and (3) an independent clustering of cells according to eye dominance.

Vertical organization

Given a set of properties of a cell, such as receptive-field position or orientation, eye preference, presence or absence of symmetry of responses to opposite directions of movement, colour coding, and so on, one can examine neighbouring cells to see whether or not they share certain of these properties. If, for example, the same value of a stimulus variable is optimal for all cells in a small region, it can be asked whether that value changes steadily or in discrete steps as one progresses through the cortex. Where the steps are discrete one can try to discover the shape and extent of the regions.

In the visual cortex a number of variables remain unchanged, or at least show no systematic trend, in penetrations extending vertically from surface to white matter. The most fundamental are the two position co-ordinates by which the retinal surface is mapped on to the cortex. This mapping is continuous. Besides this, in the monkey striate cortex, as in that of the cat, each small area dealing with a particular part of the retina is subdivided by sets of vertical partitions into several independent systems of discrete cell aggregations. One of these systems is defined by receptive-field orientation, another by ocular dominance. It seems very likely that these aggregations are columnar, with walls parallel to the vertically running fibre bundles and perpendicular to the layering pattern. The evidence for this is chiefly that sequences of cells with common physiological characteristics tend to be long in penetrations that are perpendicular or almost perpendicular to the cortical surface, and short in oblique penetrations. In the cat the most direct evidence that aggregations were columnar in shape came from multiple closely spaced parallel penetrations in which a lesion was made at each change of receptive field orientation (Hubel & Wiesel, 1963). This type of experiment was not done in the monkey, but we have no reason to think that the results would be different.

Retinotopic representation. Neighbouring cells in area 17 invariably have receptive fields in roughly the same part of the retina, and movement along the cortex corresponds to movement along the retina according to the well known retinotopic representation. We have not tried to make a detailed topographic mapping, but in a limited exploration of the dorsal convexity and ten or so additional penetrations through the buried calcarine fissure, our results agree well with Talbot & Marshall's early survey of the convexity (1941), and the subsequent extensive mapping by Daniel & Whitteridge (1961). This detailed topographic representation does not hold at a microscopic level. As in the cat (Hubel & Wiesel, 1962), the fields of successively recorded cells in a perpendicular track are not precisely superimposed: instead there is an irregular variation in field position from

cell to cell, small enough so that the fields overlap, and large enough so that, in a perpendicular penetration with fifteen or twenty fields superimposed, the area covered is about 2–4 times that of the average receptive field. In a long oblique penetration one finds some drift in field position corresponding to the gross topography, but when the component of movement along the surface is only a millimetre or so, for the part of the cortex subserving regions of retina within about 5° of the fovea, the drift is considerably less than the random staggering, and is obscured by it. In the peripheral retina the topographic representation becomes coarser, but to compensate for this the receptive fields become larger, and the situation is therefore similar.

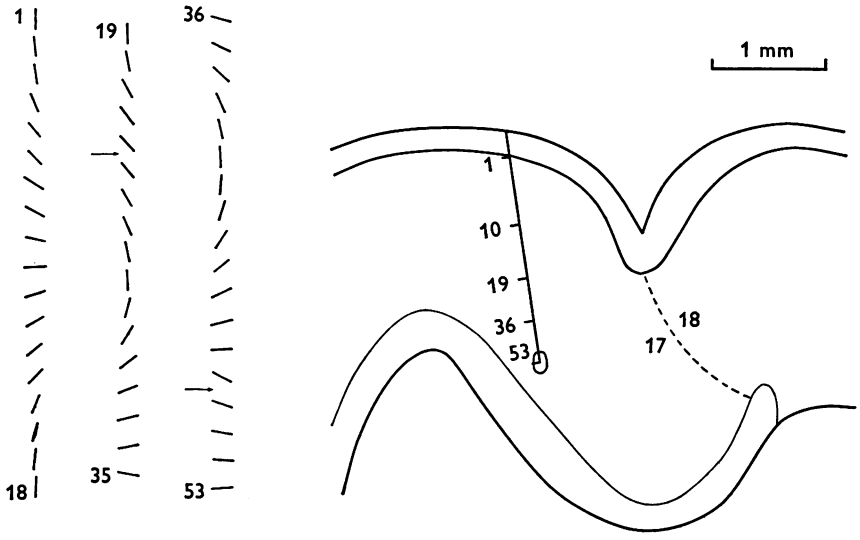
This topographic representation does not by itself constitute a columnar system even though the retinal position co-ordinates remain virtually constant in a penetration perpendicular to the cortical surface. The term 'column' as first used by Mountcastle (1957) and as it is used here, refers to a discrete aggregation of cells, each aggregation being separated from its neighbours by vertical walls that intersect the surface (or a given layer) in a mosaic. In the retinotopic projection the representation is continuous; there are no sudden jumps as the surface is traversed. It is upon this continuous topographic map that the column-systems described below are engrafted.

Receptive-field orientation. Sequences of cells with identical receptive-field orientations can be seen in Text-figs. 8, 10, 11, and 12. The sequences tended to be shorter than in the cat, and penetrations in which the same orientation was maintained from surface to white matter were somewhat less common, occurring only when the track was normal to the cortical surface or almost so. An example can be seen in Fig. 12, penetration 1. Some idea of the cross-sectional size of a column can be obtained by projecting the distance spanned by a single sequence on to the cortical surface. This projected distance was seldom more than about $\frac{1}{4}$ mm, and most sequences were considerably shorter, an average being more like 0·1–0·2 mm (see Text-fig. 10).

Ordered orientation columns. In several experiments in the cat certain regions of the striate cortex seemed to be highly organized, with changes in orientation from column to column taking place in small regular progressive steps, all in the same direction, either clockwise or counter-clockwise. Hints of such organization were seen in many penetrations in the monkey, but the sequences tended to be short. For example, in the first six cells of Text-fig. 7, five orientations are represented, each shifted about 20° clockwise compared with the previous. Following such a sequence there was often a shift of orientation in the reverse direction, perhaps followed by a resumption of the sequence for a few more steps and then

another similar interruption. Large shifts, of 45–90°, while not rare, were less common than small ones.

By far the most impressive example of orderly sequences was seen in one experiment in the spider monkey, illustrated in Text-fig. 9. The penetration entered area 17 very close to the 17–18 border, at an angle of about 30° to the normal. Fields of the first cells were oriented almost vertically.



Text-fig. 9. Reconstruction of a penetration through striate cortex about 1 mm from 17–18 border, near occipital pole of spider monkey. To the left of the figure the lines indicate orientations of columns traversed; each line represents one or several units recorded against a rich unresolved background activity. Arrows indicate reversal of directions of shifts in orientation. Histological section through first part of this penetration is shown in Pl. 2.

Subsequent cells and unresolved unit activity showed regular small shifts in orientation, consistently in a counter-clockwise direction, so that at a depth of about 1 mm, after eighteen shifts, the orientation had revolved through 180° and was again vertical. The progression continued in a counter-clockwise direction for another 45°, and then, at the point marked by the first arrow, the direction of shifts suddenly reversed. Now fifteen clockwise changes in orientation took place in the next 180°, followed by another ten clockwise shifts through almost another 180°. Finally, near the end, the process seemed to be reversing itself again, with counter-clockwise shifts beginning at the second arrow. There were, in all, 52 shifts in orientation, the smallest being about 6° and the largest around 20°, and in the course of the penetration each orientation was represented

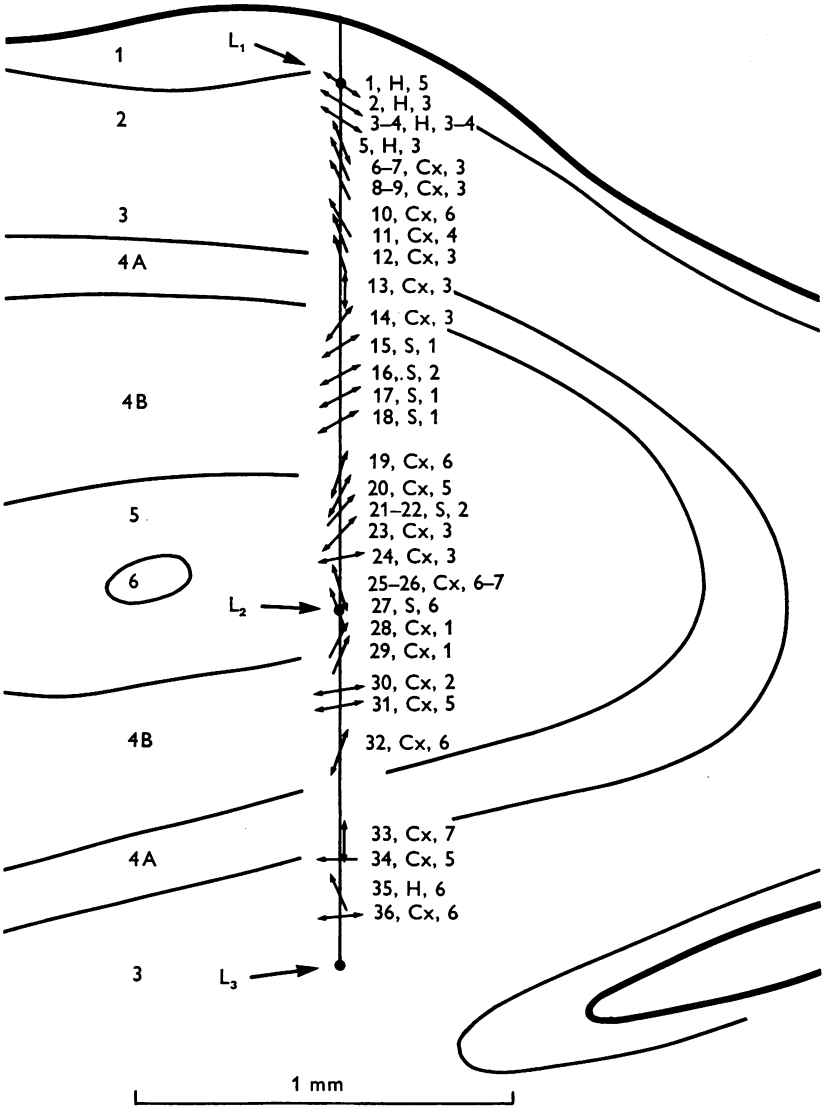
about 4 times. The field positions of the final cells were in exactly the same place as those of the first, indicating that the distance traversed in a direction parallel to the surface had been too small to produce a measurable shift in receptive field position.

In this penetration the average shift was about 13°, associated with an average electrode movement of 40 μ, or, given the obliquity of 30°, a movement parallel to the cortical surface of 20 μ. From the higher-power photomicrograph of the cortex in the area of this penetration, shown in Pl. 2, 20 μ seems to be the order of magnitude of the widths of the vertical pallisades of cells in this area. The vertically orientated striations may thus represent the actual columns of cells, at least in this experiment, and the columns must have close to the minimum possible width, since the pallisades are only one or a very few cells wide. From this degree of orderliness and the probability that a similar order would have held for any direction of horizontal movement across the cortical surface, it seems likely that columns have the form of parallel sheets rather than pillars. In the cat this sort of geometry was also suggested in one surface-mapping experiment (Hubel & Wiesel, 1963, Text-fig. 4 and Pl. 2).

Ocular dominance. In the monkey there was a marked tendency for successively recorded cells to have the same eye-preference (Text-figs. 8, 10, 11 and 12). Neighbouring cells did not necessarily fall into the same ocular-dominance group, but they usually favoured the same eye. Since there were several vertical penetrations from surface to white matter in which there was no change in eye preference, it is likely that the aggregations of cells are columnar. It is also evident that these regions of common eye-preference have nothing to do with orientation columns, the two systems apparently having entirely independent borders. Of the two types of columns, those associated with eye dominance seem to be larger, often including several orientation columns.

Aggregation of cells according to ocular dominance was first established in the cat striate cortex (Hubel & Wiesel, 1962; 1965*b*), but in the cat the organization was less clear cut, since, besides regions in which all cells had similar eye preference, there were regions of mixed allegiance, in which cells of all ocular-dominance groups, including group 4, were mingled. (For definitions of ocular-dominance groups see legend of Fig. 8.) These mixed regions tended to obscure the parcellation into columns in the cat (Hubel & Wiesel, 1962, p. 140), and indeed it was not until the columns had been accentuated by raising cats with strabismus that we became fully convinced of their existence (Hubel & Wiesel, 1965*b*). In the monkey the parcellation is far more obvious: the columns are possibly larger, mixed columns are rarer if they exist at all, and cells of dominance groups 1, 2, 6 and 7 make up a larger proportion of the population.

Direction of movement. As noted above, the monkey striate cortex resembles that of the cat in that complex cells tend to respond actively to a moving stimulus, with great cell-to-cell variation in directional selec-



Text-fig. 10. Reconstruction of an oblique penetration through striate cortex of spider monkey. This experiment indicates laminar grouping of cells according to complexity, and aggregation according to orientation, directionality of movement, and ocular-dominance. As in Text-fig. 8, 19 Cx 6 means 'Unit 19, complex, ocular-dominance group 6'.

tivity—some firing actively to diametrically opposed directions, others responding to one direction and hardly at all to the other, and still others with various degrees of intermediate directional asymmetry. There is some intermixing between these groups, in that two simultaneously recorded cells are often driven by opposite directions of movement (Hubel, 1958). In the present series there nevertheless appeared to be some grouping of cells according to the presence or absence of directional preference. In most penetrations there were sequences, sometimes long ones, in which all cells showed strong directional preference, followed by sequences in which the cells all responded well to both directions of movement. This is seen in Text-fig. 10, which illustrates a penetration cutting across a gyrus in the spider monkey. Cells 1–5, 13–20, 23–27, 30–33, were all bidirectional, whereas those of sequence 6–12 were unidirectional. There may thus be another independent, perhaps columnar system of cortical subdivisions, this one dependent on symmetric *vs.* asymmetric responses to movement.

Finally, there was some indication of a grouping of cells according to their preference for stimulus form—slits, edges, or dark bars. Colour coded cells similarly often came in clusters. The shape of the aggregations for these systems is not clear: they could be nests or columns.

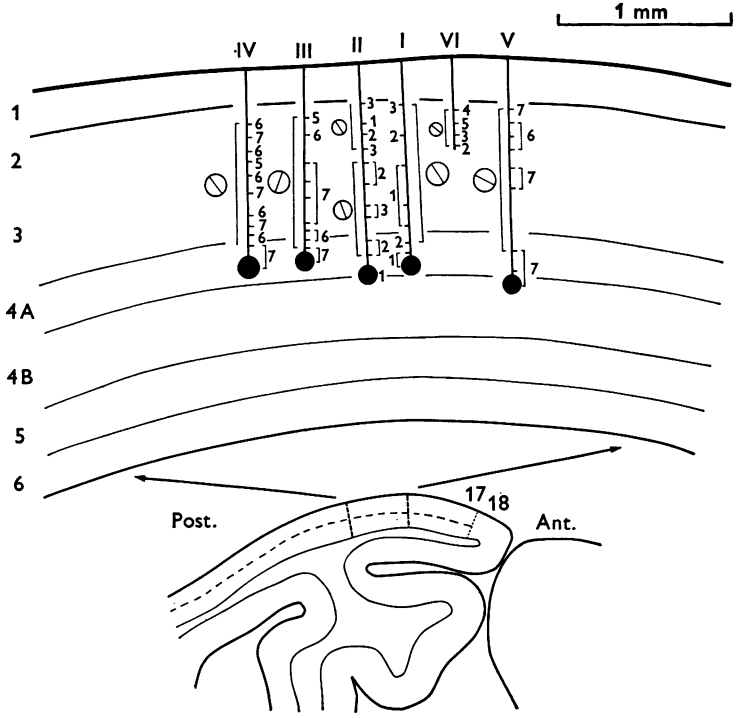
Horizontal organization

The most conspicuous anatomical feature of the striate cortex is its rich layering—indeed it was so named for that reason. From the outset it has been clear that there are differences from layer to layer in the physiological properties of cells in area 17. These differences are more prominent than in the cat, just as the histological differences in layers are more prominent. In five experiments done specifically to investigate the layering differences, fourteen penetrations were made, six through the full cortical thickness and eight to the 4th layer. Two experiments, to be discussed in more detail below, are illustrated in Text-figs. 11 and 12, and the results from all rhesus experiments are tabulated in the histograms of Text-figs. 13 and 14.

Receptive field organization. In the second layer and upper part of the third almost all of the cells were complex or hypercomplex, and as a rule the optimum stimulus orientation was precisely defined. We found no simple cells in layer II, and in III they occurred only in the deepest parts, close to IV. On entering this border zone and crossing into upper IV the first simple cells appeared, hypercomplex cells were no longer seen, and in complex cells the orientation specificity began to relax, with brisk responses over a wider range of orientations to either side of the optimum, but still no response at 90° to the optimum.

Usually in IV A, but sometimes only on entering IV B, a sudden change

took place in the unresolved background activity: it became more prominent, higher in pitch, and lost all trace of orientation preference. Text-figure 11 and Pl. 3 illustrate an experiment done expressly to determine the depth at which the background lost its orientation specificity. In each



Text-fig. 11. Six closely spaced parallel penetrations through rhesus striate cortex made to determine the layer in which background and some units lacked orientation specificity, and in which most cells were driven by one eye exclusively. Lesion made in these regions are indicated by black circles. Lines within the open circles indicate optimum stimulus orientation. Numbers to right of each penetration refer to ocular dominance group of each isolated unit.

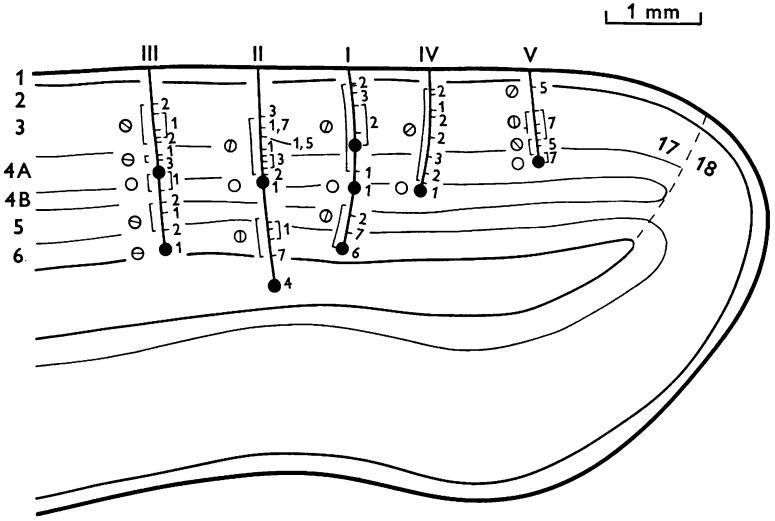
penetration this point was marked by a lesion, shown as a filled circle. All lesions were in IV A or near the IV A–IV B border. A similar experiment, with the same outcome, is illustrated in Text-fig. 12. Here the points of appearance of non-oriented background are shown to the left of each penetration by open circles.

Throughout IV B there was a mixture of simple cells and units which lacked orientation specificity. This was the layer with the fewest complex units and the most non-oriented ones (Text-fig. 13). In V and VI the background again became selectively responsive to specifically oriented

lines, and the units were mainly complex, with some hypercomplex ones intermixed.

Some of these laminar differences in field types are illustrated also in Text-fig. 10.

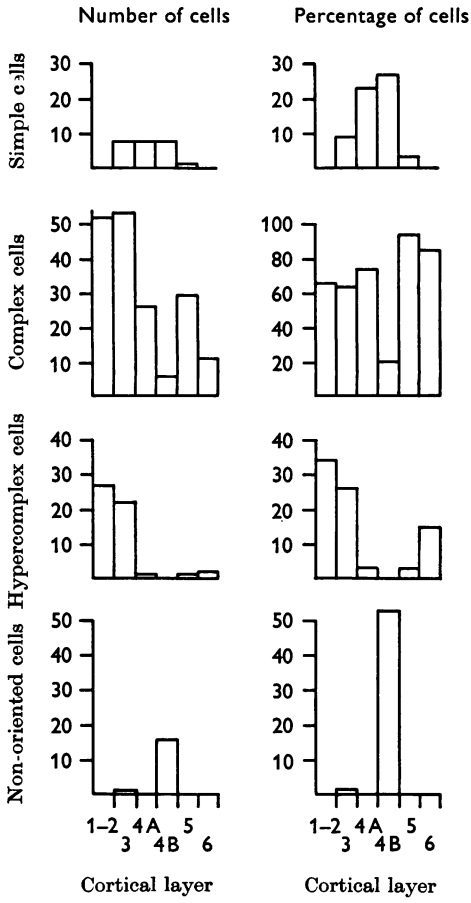
Binocular interaction. One marked difference between layers was related to binocular interaction. This is illustrated in the histograms of Text-fig. 14, and in Text-figs. 11 and 12. At the beginning of a typical penetration



Text-fig. 12. Five close-spaced penetrations in rhesus area 17. Open circles indicate a lack of background orientation specificity; other conventions as in Text-fig. 11.

one eye or the other was consistently dominant, and through layer II and most or all of III one encountered a mixture of cells in groups 2 and 3 with a few from group 1, or else a mixture of 5 and 6 with an occasional group 7. At some stage, usually in upper IV, but occasionally as deep as the border of IV A and IV B, the eye that had been non-dominant would drop out completely, and through the remainder of layer IV cell after cell would be in group 1 instead of 2 or 3, or group 7 instead of 5 or 6. This was just the point at which the background became poorly oriented (i.e. the regions marked by lesions in Text-figs. 11 and 12). Simple cells recorded here were almost always groups 1 or 7, but a few exceptions were seen in groups 2 and 6 and there was a single group 4 simple cell. In penetrations that extended through most of the cortical thickness, binocularly driven units remained scarce as layer IV was traversed, but reappeared abruptly in layer V, and persisted throughout V and VI.

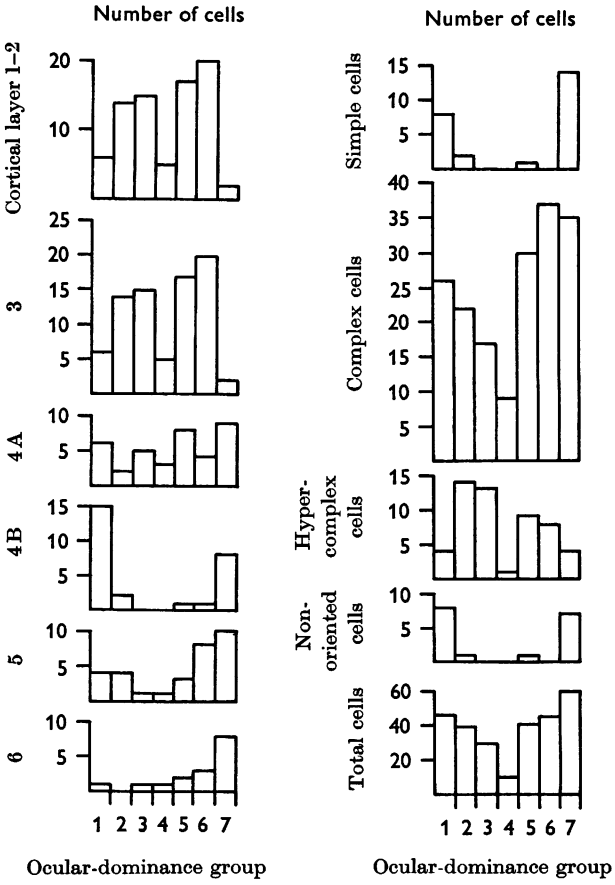
Finally, ocular-dominance differed markedly with cell type (Text-fig. 14). This is not surprising since both ocular dominance and cell type tended to vary from layer to layer. There was an increase in binocular interaction in going from simple to complex and from complex to hypercomplex, with



Text-fig. 13. Histograms of 272 cortical cells showing numbers of the different cell categories, in each layer. Only the cells from rhesus monkeys are included. In the right-hand set of histograms, cells are expressed as a percentage of the total number in a given layer.

groups 1 and 7 becoming rarer, and the intermediate groups more common. But in general cells driven equally by the two eyes were less common in the monkey than in the cat, most monkey cells falling in groups 1, 2, 6 and 7. The ocular-dominance distribution of cells in the cat is closer to that of monkey area 18, than to monkey 17 (unpublished). These results

suggest that in monkey striate cortex impulses from the two eyes probably converge not so much on the simple cell, as occurs in the cat, but chiefly on the complex cell.



Text-fig. 14. Left: Distribution of 272 rhesus cells among the various layers according to ocular-dominance group. Right: Distribution of 272 cells among the different cell-classes, according to ocular-dominance group.

DISCUSSION

From this and previous studies it is clear that any small region of the striate cortex analyses some small part of the visual field in terms of the direction of light-dark contours (in particular, the tangent to the contour lines), a detection of movement of the contours, a registration of the type of contour (light against dark, edge, and the like), and, at the hypercomplex level, a detection of any change in direction (curvature) of the contours. At any one time only a small proportion of cells are likely to be

influenced (activated or suppressed), since contours of inappropriate orientation and diffuse light have little or no effect on a cell.

Hypercomplex cells, which we had thought occurred only in 18 and 19 in the cat, turn out to be fairly common in 17, both in cat and monkey. Presumably in early studies their presence was not detected because they gave no response to a line that was too long, or perhaps they were classed as complex when they responded well to a line that happened to be the correct length. For these cells the proportion responding to a given contour must be extremely small, since even an appropriately oriented line is ineffective if it maintains that orientation over too great a distance.

The elaboration of simple cortical fields from geniculate concentric fields, complex from simple, and hypercomplex from complex is probably the prime function of the striate cortex—unless there are still other as yet unidentified cells there. One need not assume, of course, that the output consists entirely of the axons of hypercomplex cells, the other types being merely interposed as links between input and output. We know, for example, that in the cat the posterior corpus callosum contains axons of all three cell types (Hubel & Wiesel, 1967).

A second function of the striate cortex concerns the convergence upon single cells of input from the two eyes. At the geniculate level any binocular interaction must be relatively subtle, since no one has yet mapped out receptive fields in the two eyes for a single geniculate cell, as can be done routinely for cortical cells. In the cortex stimulation of both eyes in corresponding parts of the receptive fields usually gives a greater response than stimulation of either eye alone. In the monkey as in the cat, this convergence takes a special form in which the influence of the two eyes is combined in varying proportions in different cells. Indeed, in the monkey the process of amalgamation of the two inputs is further delayed, so that interaction is minimal for simple cells, distinctly more for complex, and possibly still more for hypercomplex.

Given that contour analysis and binocular convergence are two prime functions of striate cortex, the parallel and independent manner in which the processes are carried out by this structure is worth noting. For both functions columns are the units of organization. In a given 'eye-preference' column one eye is emphasized, in the next the other eye. In a superimposed but quite independent system, one 'orientation' column subserves one orientation, another column a different one. In both types of column the contour analysis and binocular convergence occur in a vertically interconnected system of layers, with the earliest stages in IV B, the latest ones in II and III, and probably also in V and VI. Thus IV B is made up chiefly of simple cells and units (possibly afferent fibres) that show no orientation preference, and these are almost all monocularly driven, whereas in II and

III one finds complex and hypercomplex cells, mostly binocularly driven. This difference by layers in complexity of responses and in binocular interaction is entirely consistent with the Golgi type anatomy of Cajal (1911) and Lorente de Nó (1943), since in terms of connexions cells of layer IV are closest to the input, and the upper and lower layers are furthest away. It is hardly surprising that physiologically the populations of individual layers are not pure, in view of the mixture of morphological cell types in each layer, and the presence of axons passing up and down from other layers. In the cat the layering is less distinct, and the tendency for each layer to contain a mixture of cell types seems to be greater—in any case the physiological evidence for segregation of different cell types in different layers, while suggestive in the cat (Hubel & Wiesel, 1962), was not nearly as clear as in the monkey. The present demonstration of a clear difference in function between cells in different cortical layers is, of course, only a first step toward the goal of correlating histologically defined cell types with function.

The form taken by the two systems of columns deserves some comment. The existence of regions in which orientation columns are highly ordered continues to be baffling, for if there are two kinds of striate cortex, one ordered and the other not, the anatomy gives no hint of this. There is a suggestion that the narrow orderly columns may sometimes correspond to the radial fascicles seen microscopically, but these are seen everywhere in 17, and the ordered regions seem not to be present everywhere. Where columns are ordered, it seems likely that they are very long narrow slabs, perhaps not straight, but swirling, if one can judge from the reversals in shifts seen in Text-fig. 9. It is possible that these ordered regions may be more common than we realize, for their detection depends on rather ideal recording conditions in which the electrode moves forward steadily rather than in jumps, and records activity at all times. The possible purpose served by such an ordered system of columns has been discussed elsewhere (Hubel & Wiesel, 1963).

In view of the recent work of Campbell & Kulikowski (1966) showing a difference in ability of humans to discriminate between horizontal or vertical lines and oblique lines, we have looked for any differences in the occurrence of horizontally and vertically oriented fields as opposed to oblique fields, but have seen none, in cat or in monkey. The problem is presumably one of comparing the frequency or size of the various orientation columns, and our series is doubtless too small to permit this, especially if one wishes to detect a difference of a few per cent. At least it is clear that horizontal and vertical orientations are not many times more common than others.

In the binocular columnar system the columns seem to be coarser, and take a special form. At the level of layer IV B there is a mosaic of alter-

nating left-eye and right-eye representation, each apparently almost pure. This presumably simply reflects the tendency for afferents to the cortex to be grouped (Hubel & Wiesel, 1965*b*), as is so for the columns of the somatosensory cortex described by Mountcastle (1957). As the visual input is transmitted over several stages to the more complex cells in the upper and lower layers, there must be progressively more intermixing between the eyes, presumably by interconnexions that run obliquely. The columns nevertheless remain discrete, with almost all cells in one column favouring one eye, though no longer dominated completely by it. There do not seem to be regions of mixed dominance, as one finds in the cat. For the binocular columns the physiological evidence thus indicates that there is some interchange between one column and its immediate neighbours, minimal in layer IV, but increasing in the superficial and deep layers. (By definition two adjacent binocular columns must favour opposite eyes.) This is in sharp contrast to the orientation columns, since for these there is no evidence to suggest any cross talk between one column and its immediately adjoining neighbours. There is of course no reason why an orientation column should not have rich connexions with another column of identical field orientation even though the two may be separated by as many as 15–18 different columns. Indeed, if eye-preference columns are interconnected, and if one eye-preference column does contain many orientation columns, then the interconnexions must be highly specific, one orientation column being connected to another some distance away. These suggestions depend of course on rather indirect inferences from physiological experiments, but they may have some value in indicating certain patterns of connexions to look for with morphological techniques.

If there are indications that the orientation columns take the form of parallel pillars, or, in more ordered areas, parallel slabs, we have no hints at all about the shape of the eye-preference columns. They differ from the orientation columns in being of just two types, instead of more than a dozen, and the two should be about equally prominent, given the lack of any marked dominance of one eye or other in the cortex as a whole. One would therefore expect a patchwork of alternating columns like a checker board, or a confluent matrix of one type with pillars of the other type embedded within it, or a series of parallel slabs. These possibilities are mentioned here because the term 'column' itself implies a series of pillar-like structures, which is probably the least likely form in this case.

The columnar system seems to represent a method by which many areas of cortex—somatosensory (Mountcastle, 1957) visual, including 17, 18 and 19, and perhaps motor (Asanuma & Sakata, 1967)—deal with multi-dimensional problems using a two-dimensional surface. In the visual system the two co-ordinates of the visual field are mapped on the two

surface co-ordinates; other variables, notably line orientation, eye dominance, possibly movement directionality, are handled by subdividing this surface into overlapping mosaics which are independent, just as the picture of a jigsaw puzzle is independent of the borders separating the pieces. With two such mosaics known and a third suspected, it will not be surprising if more are found in the future.

To conclude, it is easy to draw up a large list of gaps still to be filled in our understanding of this structure. To mention only a few, the binocular interaction we have described tells us nothing about mechanisms for handling stereoscopic depth perception. Bishop's group in Sydney and Barlow's in California have evidence for horizontal non-correspondence of some cells in cat area 17, and the relation of these to the binocular mechanisms described here for the monkey will be most interesting. Our knowledge of cortical colour mechanisms is still very sketchy. Anatomically one is just beginning to understand the layering of the cortex, and some features, such as the significance of layers I, V and VI are still a complete mystery. At a synaptic level the correlation of structure with physiology, as is now being done in the retina (Dowling & Boycott, 1966), is still lacking in the cortex. The part, if any, that area 17 plays in attention mechanisms in conscious animals is completely obscure. But despite the large areas still unexplored, in broad outline the function of area 17 is probably now relatively well understood. One knows roughly how the output differs from the input, and it is possible to make guesses that can be tested concerning the circuits that underly these transformations. Knowing what image is falling on the retina at any given moment, one can predict with some confidence what most types of cells will be doing.

Specialized as the cells of 17 are, compared with rods and cones, they must, nevertheless, still represent a very elementary stage in the handling of complex forms, occupied as they are with a relatively simple region-by-region analysis of retinal contours. How this information is used at later stages in the visual path is far from clear, and represents one of the most tantalizing problems for the future.

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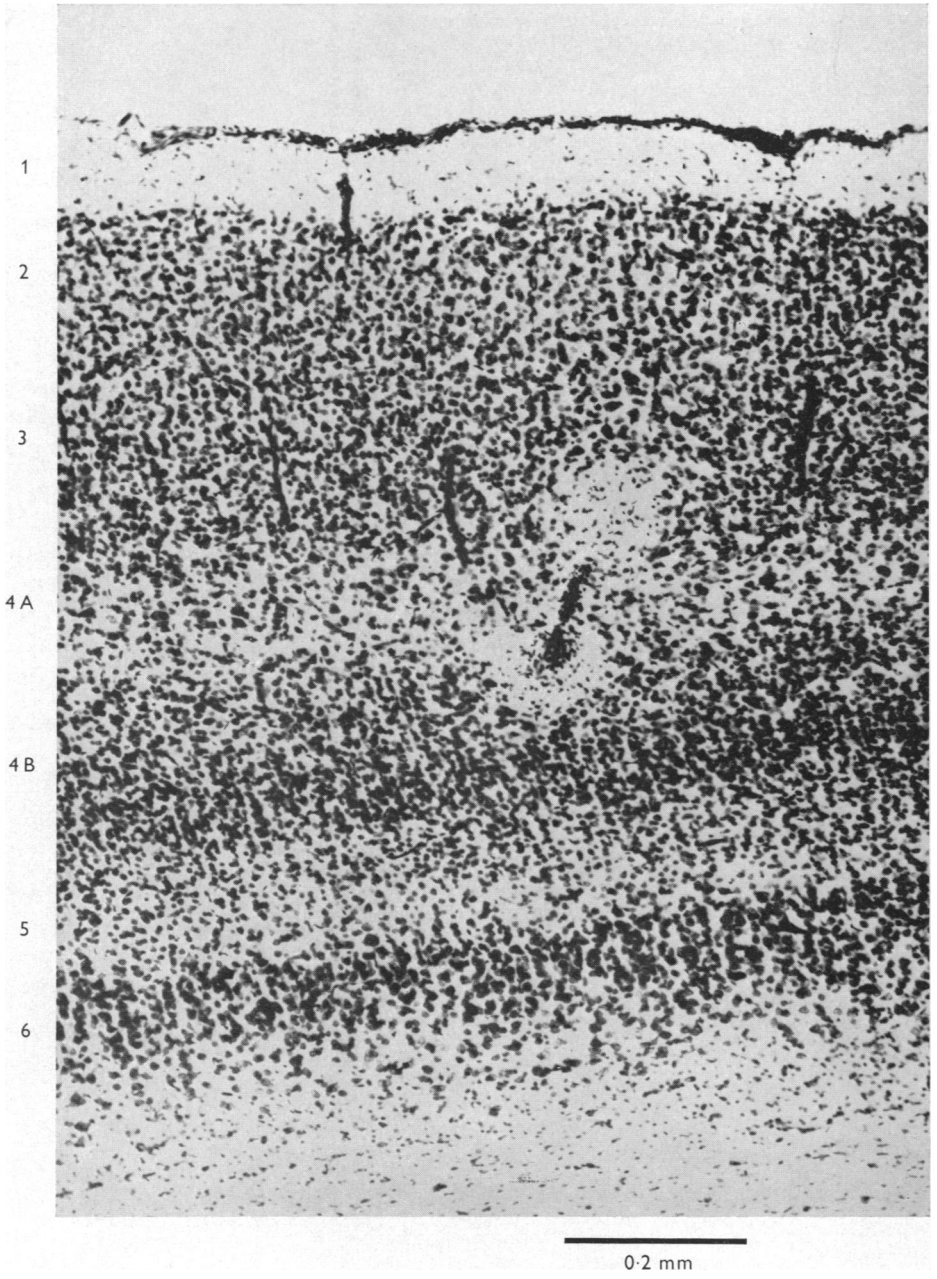

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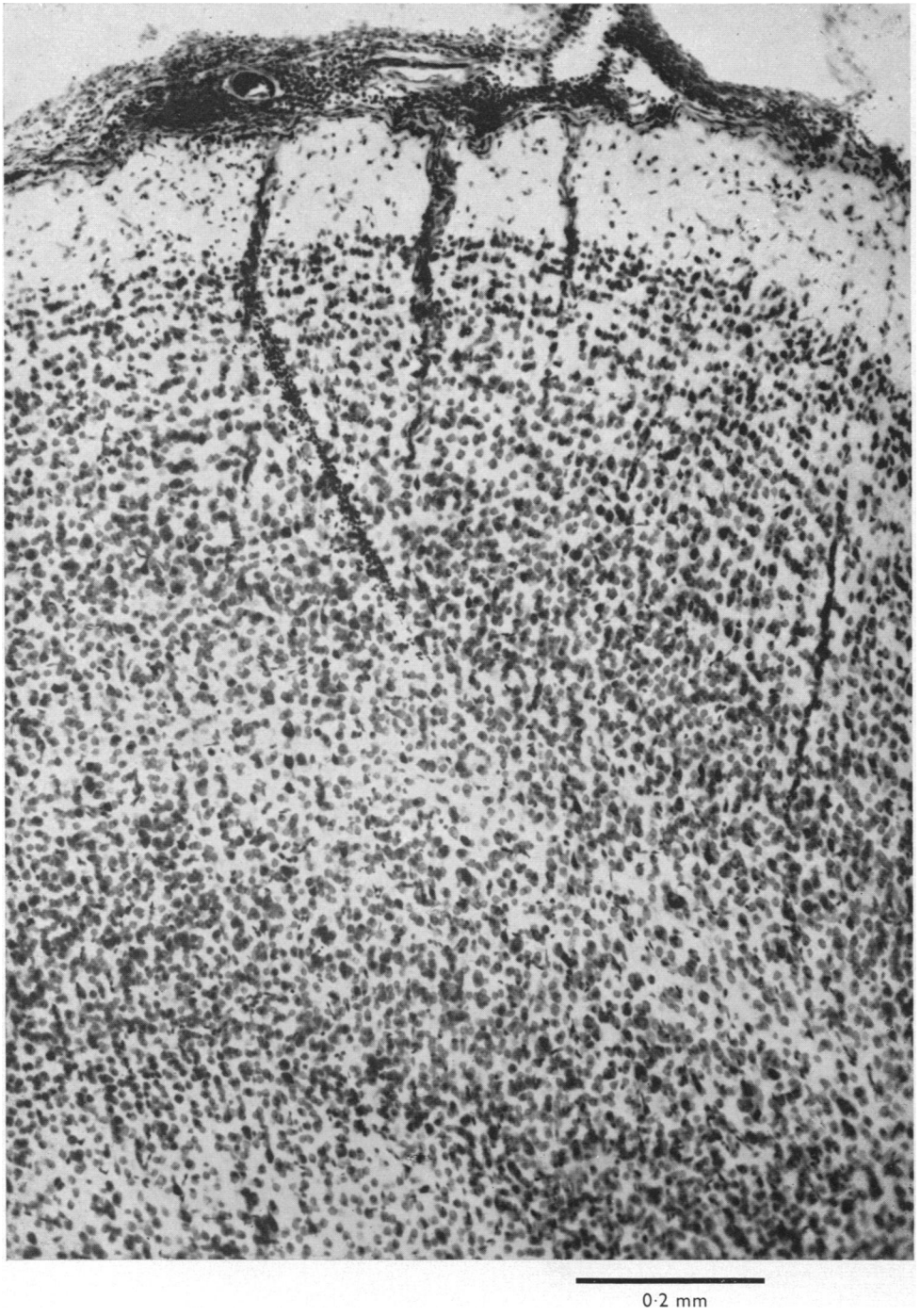
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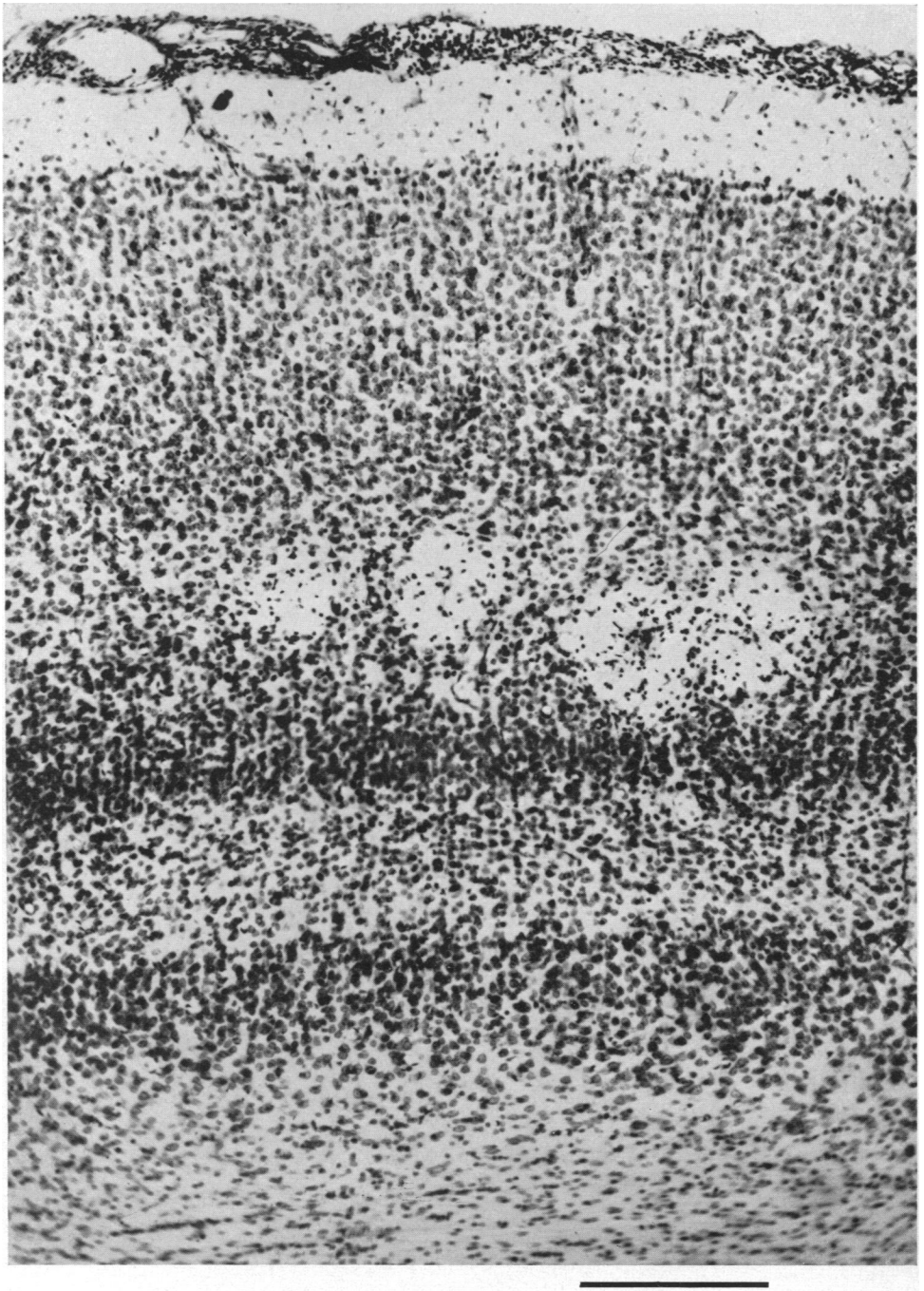
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EXPLANATION OF PLATES

PLATE 1

Nissl-stained section corresponding to the experiment of Text-figs. 7 and 8, showing part of penetration and two lesions. Layers are indicated to left.

PLATE 2

Nissl-stained section through the electrode track of Text-fig. 9, showing first part of the track outlined by inflammatory reaction.

PLATE 3

Nissl section showing four of the five lesions of Text-fig. 11.